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THE FUNCTIONS OF THE NERVOUS SYSTEM, WITH SPECIAL REGARD TO RESPIRATION, IN ACRIDIDÆ.

BY HENRY Z. EWING.

From the physiological laboratory of the University of Kansas.

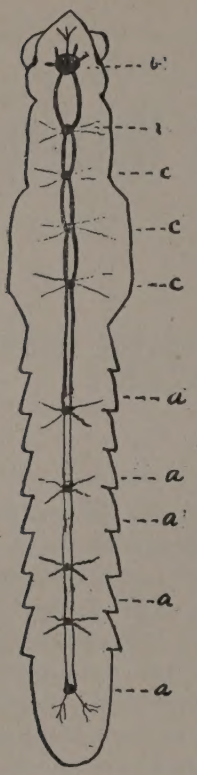
IN my experiments I have not confined myself to any one species of the Acrididæ, but have used any of the common ones that could be easily obtained, especially different species of the grasshoppers, *Melanoplus differentialis*, *Dissosteira carolina*, *Melanoplus femur rubrum*, and *Brachystola magna*, the latter being an especially good species for experimentation, because of its size. I have not noticed in results of experimentation in the different species any differences that might not have been observed in individuals of the same species.

Of the literature bearing upon this subject, Bethe's work[1] is perhaps the most important. I was able to corroborate many of his observations on the grasshopper, and with abundant material, while he had but few animals to experiment on.

My work is not all new, yet I think those facts which I have been able to add to those previously determined, justify me in offering this paper for the consideration of those interested in insect physiology.

Before proceeding with my subject proper, I shall briefly describe the respiratory and nervous systems of the grasshopper, in order to make my paper intelligible to those unacquainted with the anatomy of this insect. The three principal parts of the respiratory apparatus are the spiracles, air-sacs, and tracheal tubes. There are twelve spiracles on each side, three thoracic and nine abdominal. By means of these and the trachea an interchange of air takes place. One very large pair of air-sacs is situated in the thorax and five abdominal pairs arise

1. Bethe, W. Pflugers, Archiv fur die Gesammte Physiologie, 1897, vol. 68, p. 494.



NERVOUS SYSTEM OF THE GRASSHOPPER.
Diagramatic.

a. Abdominal Ganglia.
d. Infra-œsophageal Ganglion.
b. Supra-œsophageal Ganglion or Brain.
c. Thoracic Ganglia.

directly from the spiracles. In addition to these superficial air-sacs there are very many, probably several hundred, distributed throughout all parts of the body. Of the tracheal tubes there are two main trunks on each side. One is placed above and the other below the plane of the alimentary canal. They communicate with each other and with the air-sacs and spiracles. Besides these large trunks there are countless ramifications to all parts of the body, communicating by their finest twigs with internal cells. The oxygen of the air is thus separated from the fluids of the body by a very delicate endothelial membrane.

The respiratory movements in the normal grasshopper consist of an expiratory and an inspiratory phase. During inspiration the active contraction of the abdominal muscles produces an increase in the breathing space, in that the antero-posterior and dorso-ventral diameters of the abdomen are increased, and air passes in through the open spiracles to fill the air-sacs, since the pressure within, in consequence of the formation of a partial vacuum, becomes less than atmospheric. In active or forced inspiration, the abdomen may be elongated, and by a forward and backward movement of the head, the air-spaces in the abdomen may be still further increased. Expiration is a passive movement; that is, the muscles relax and the breathing space is decreased as the abodmen relaxes by its own elasticity. At the same time the return of the abdominal segments to closer contact with each other, forces the contents of the air-sacs along the tracheal tubes into their finer ramifications, and also expels air that has been in contact with the fluids of the body into the air-sacs and thus to the exterior of the body.

The nervous system of the grasshopper consists of a supra-

œsophageal ganglion or brain proper, and a double chain of ganglia on the ventral side of the body, composed of one sub-œsophageal, three thoracic and five or six abdominal ganglia connected by a double nerve fibre with each other and with the brain. Each ganglion consists of two halves intimately united by a transverse commissure.

The experiments, in the course of which the following notes were made, consisted in removing or severing, by means of fine, sharp, curved or straight scalpels or scissors and hooked forceps, different parts of the nervous system of the insect. The nervous system had been carefully studied and outlined in relation to definite landmarks on the exterior of the body. During the operation the animal was held in an insect holder, while the parts of the nervous system were exposed and removed with aseptic precautions. The regions from which parts were removed were examined under the microscope, to ascertain whether more or less of the planned lesion had been executed. The chitinous piece was replaced then over the wound and held in place by shellac or wax cement. The insects were kept under fairly constant external conditions throughout the period of observation. A post-mortem was made in most cases.

My work was pursued under the supervision of Professor Hyde, of the physiological department, to whom I am indebted for much valuable assistance.

I. Extirpation of the Brain.

The rate of the respiratory movements was slowed, otherwise this operation has no marked effect upon respiration. Pinching the antennæ, which, after the brain is removed, remain motionless in any position in which they are placed, produced no reflex movements. There are evidently no sensations left in these organs, although the grasshopper would still stroke them with his front feet, as the normal animal occasionally does to clean them. Bethe observed this action and thinks that in the operation a stimulus is aroused in the inferior œsophageal ganglion that is similar to a stimulus produced by the antennæ in the intact animal. The head is lowered sideways, the fore leg is stretched toward the region where the antenna is normally found. Contact with the antenna causes the foot reflexly to take an increased hold on it and to press it to the ground, as if to prevent the escape of the seemingly foreign body. The

pull thus executed reflexly causes the head to be raised. When I cut off one antenna from a normal hopper the head was bent, the fore leg extended to where the antenna normally was and the wound rubbed. When the other antenna was removed the insect rubbed first one then the other side of the head where the wound was, going through the different phases of the reflex acts noticed in the case above, first with the front leg of the one side and then with that of the other side. This, in part, proves that Bethe's interpretation of the behavior was correct, and that as the result of the operation a stimulus was created that caused the front legs to remove the irritant.

Faivre[2] considered the supra-œsophageal ganglion of the beetle, the seat of spontaneous movements, direction, and will; and Ward[3] that in the crayfish it was comparable to the cerebellum of vertebrates, since its loss is followed by the disappearance of spontaneous activity. Lemoine,[4] Treviranus[5] and Burmeister[6] regard the supra-œsophageal ganglion of arthropods the seat for spontaneous movements; and Leidig believes that the supra- and sub-œsophageal ganglia together are analogous to the brain of vertebrates. On the other hand, Yersin[7] observed that a cricket occasionally moves spontaneously after its brain or supra-œsophageal ganglion has been destroyed. Bethe affirms that the brain, besides being the seat of peripheral nerves, the centre for inhibitory reflex movements, and for controlling the tonus of the muscles, (each half of the brain exerting its influence over its own side,) is not the special centre for spontaneous movements, inasmuch as spontaneous movements were not lost in those arthropods that had their supra-œsophageal ganglion extirpated. The spontaneous activity after the loss of the brain was, however, least observed in the grasshopper.

Added to this, Faivre, Ward and Bethe noticed that when the brains of the arthropods that they investigated were extirpated or separated from the other parts of the nervous system, the animals lifted their bodies above the normal level by increased contraction of the flexor muscles, whereby the legs were flexed

2. Faivre.—Comptes rendus, 1860, T. 51.
3. Ward, J.—Journal of Physiology, 1879, vol. 2, p. 214.
4. Lemoine.—Ann. d. scienc. natur., 1868, T. 9, p. 100.
5. Treviranus.—Die Erscheinungen des Organischen Lebens, Bremen, 1832.
6. Burmeister.—Handbuch der Entomologie, Berlin, 1832.
7. Yersin.—Bulletin de la Soc. Vaudoise d. sciens. natur. 1856, T. 5, p. 284.

at the joints and the body raised. Bethe observed this abnormal flexed condition of the appendages to pass off in the grasshopper after twenty-four hours, when the normal position of the body was practically assumed again.

I found that brainless grasshoppers continue to move their palps and occasionally wipe or preen the palps with their front legs for apparently no cause. Shortly after the operation they make a few spontaneous walking movements, that gradually become weak and wavering, so that during twenty-four hours it may be that they have only turned round, or taken one or two steps. During this time, however, they execute peculiar swaying movements, whereby the legs of first one side, then the other, are slightly raised from the ground. Similar movements are frequently observed however in the normal hopper.

The normal grasshopper stands with its body quite close to the table, the femur of the hind legs obliquely bent upwards, while the brainless animal assumes the position described by Bethe. By close inspection it is seen that, shortly after the loss of the brain, the two pairs of walking legs are flexed at the joints, so that they assume a straighter position, and point toward the median plane of the body instead of away from it. Thereby the thorax is elevated, while the jumping-legs are no longer held obliquely with the abdomen but more parallel to it. In addition to this, it is observed, that the head is lowered so that the palps touch the table. During the following hours, however, the flexed condition of the legs gradually disappears, and they assume finally an abducted posture, so that the abdomen rests on the table and the walking legs are more extended from each other.

Usually, when a normal hopper is taken in the hand, the respiratory movements cease for a few seconds, being inhibited through the stimulus of touch or temperature of the fingers. This inhibition is not observed in the brainless hopper, under this circumstance. I found, moreover, that for about one hour after the brain is destroyed, the slightest touch will often cause the animal to fly or hop, a much stronger touch being normally required to excite this response. It may either jump once for each stimulus, or take one or two steps and then stop. If its wings are held with forceps it makes a weak attempt to walk away, but it does not jump or endeavor to remove the annoying

stimulus. Upon freeing the wings it takes a step or two, then stops. Though the legs follow their normal order in walking, they may first be lifted and flexed in a peculiar way before they are placed on the ground. It is further shown, that coördination is not destroyed, in that the hopper alights in quite a normal manner after a hop, and when placed on its back turns over in a perfectly coördinated manner, though seemingly exhausted from the effort. It must be added that it, as well as the normal hopper and crayfish, will remain on its back, as if hypnotized, if placed there with greatest care and careful handling.

If the palps are touched with a blade of grass, the mandibles and maxillæ begin to move, but no grass is bitten off, and sugar-water or soaked raisins, which normally are never refused, are no longer tasted or swallowed. Pinching the palps slightly causes them to move, and if acid is put on the palps it is at once rubbed off by the front legs. If the hopper is placed on a blade of grass held vertically, it will attempt to climb upon it by taking one or two steps upwards, and will cling there, but only for a short time, as it soon becomes exhausted from the effort. If one foot is pressed it takes a step in the direction of the non-stimulated side. Bethe observed that after the brain was removed these animals fluttered their wings rhythmically, but never rose higher than the level from which they started; but I have seen them fly much higher shortly after the brain was destroyed.

When all but a narrow strip of nerve tissue from which the optic nerves arise is removed from the brain tissue, the insect hops, flies and walks incessantly for hours, keeping its head close to the table, its abdomen high above it, and when it alights from hopping, it seems to have lost all sense of equilibrium, or is completely exhausted. In this case the sight may have been destroyed, and this fact may interfere with its equilibrium, while inhibition of motion may be due to a constant stimulus produced by the operation. Muscular weakness or loss of tone may explain the abnormal position of the head retained by the animal. Grasshoppers operated on in this way, behave more like those arthropods that Bethe investigated, since extirpation of their entire brain caused spontaneous and prolonged activity. The above observations show that in the

brainless grasshopper spontaneity persists only to a slight extent. The preening and palp movements, the occasional lifting of the legs of first one side then the other, and the progressive movements of a step or two during twenty-four hours, are activities produced without any apparent external cause and may be regarded as spontaneous.

Moreover, Bethe has demonstrated that in brainless arthropods the power to inhibit reflex movements is lost. They respond to stimuli too slight to elicit reflexes in normal animals, and keep up constant preening and masticating movements and varied activities of the legs; while some, as for instance the water-beetle, not only retains its progressive locomotor movements, but walks incessantly. I observed that the brainless hopper has also lost the power to inhibit reflex movements. It also exhibits the palp and preening movements, as well as the restless lifting of the legs, and responds to the slightest touch by hopping, but it does not make progressive locomotor movements of more than one or two steps during twenty-four hours, and its respiratory movements are no longer inhibited when it is first taken in the hand.

The change in flexion of the legs, followed by the weakened condition of the body, manifested by resting its head against the table, and the quick exhaustion after any effort, indicates, as will be pointed out later, that the brain exercises a control over tension of the voluntary muscles.

Coördination, however, as well as direction, still persists with the loss of the brain, since the hoppers in walking move their legs in normal order, turn over if placed on their backs, can hop, fly and alight in a normal manner, and move toward the unstimulated side when a leg is pressed.

II. Removal of Half of the Brain.

Extirpating half of the brain, by every operative precaution above spoken of, produced no material change in the respiratory movements, and the spiracles of both sides moved in the normal member. If the right half, for instance, is destroyed, sensation persists in the left, not in the right antenna, and the abdomen is curved toward the left side. The right walking-legs are flexed, so that the animal stands higher on the operated side, while the right jumping-leg is extended and, in walking, seems to propel the right side of the body onward. The wing

on the injured side is folded; that on the uninjured is partly spread. The animal may have been sluggish before the operation, but immediately afterward it is very active, moving in a circle toward the uninjured side. If it is placed on a table, with its left side very close to the edge, and stimulated, especially by touching the palps on the operated side, which are now more sensitive and produce more marked reflex responses than those on the unoperated side, it will at once fall from the table. The direction in which the animal hops may be either toward the left or the right, but shortly after the operation it hops usually toward the unoperated side. When placed on its back it turns over, but not so readily as does the normal animal.

About five hours after the loss of half of the brain, it is noticed that the hopper stands more erect; that is, inclines less strongly toward the unoperated side, and, by close inspection, it is seen that the legs on the operated side are not flexed so much as they were. Pressing either palps, wings, legs or the irritable antenna now causes the animal to move in a nearly straight line. Yersin and Bethe observed that insects that had half of the brain destroyed would gradually lose the inclined posture and respond finally to a strong stimulus by going either to the right, left or straight forward, depending upon the region stimulated. Bethe believes that the appendages on the operated side are weaker, and their reflexes are less inhibited than those on the unoperated side. His explanation is that the brain exercises a tonus over the muscles and an inhibition over reflex movements. When half of the brain is removed, therefore, the muscles on the operated side lose their tonus, become weaker, and the reflex responses are no longer inhibited, as they are in the normal animal. This view would explain some of the results of lesion to half the brain, but it does not entirely explain why the flexed position on the injured side gradually disappears. It seems that the flexors of the injured side and the extensors of the uninjured side, are stimulated; or that the extensors of the operated side and flexors of the unoperated side are inhibited, or have lost their tonus. Moreover, it seems that the same region of the brain controls these muscles which normally act together for a definite movement, and are associated and situated on opposite sides of the body, as, for instance, the flexors of one side and extensors of the other. As a conse-

quence of the unsymmetrical posture of the appendages, the animal moves in a circle.

III. Extirpation of the Subœsophageal Ganglion.

Removal of the subœsophageal ganglion is attended with much difficulty, but with great care it was removed without loss of much blood. The wound was closed with shellac. The loss of this ganglion does not stop the respiratory movements. The respiratory centre is therefore not located in this part of the nervous system, which is therefore not analogous to the medulla in vertebrates, as Faivre and others maintained. The spiracles of the abdomen and thorax continue their activity at a slower rate, and, as in the normal animal, the abdominal and thoracic spiracles often do not keep the same rhythm. Moreover, some of the spiracles on one side of the thorax may be motionless, while those on the opposite side are active. This is explained by the fact that each half of the ganglion innervates its own side of the body. The relation, however, between the two halves is so intimate that they usually act together in producing ordinary movements. The palps remained motionless; when they were strongly pinched they did not respond.

Shortly after the operation the head droops and touches the table, and the antennæ may remain in the position in which they are placed, *e. g.*, one pointing anteriorly and the other posteriorly. It hops but does not walk unless it is irritated. It remains for about an hour in any position in which it is placed, after which the shock effect passes off. If any part of the thorax or abdomen is pinched, reflex movements of the different parts posterior to the injury are observed, but no reflexes of parts anterior to the cut follow. It moves spontaneously after two hours, dragging its body along as if it were a heavy load. Its first pairs of walking-legs are abnormally flexed, and therefore do not coördinate in a normal manner with the others. This is because their nerve fibers were injured or stimulated by the operation. If it meets an obstacle it may fall over on its side, but immediately, though awkwardly, rights itself. In all the movements there seem to be a lack of perfect coördination for at least twenty-four hours.

Faivre believes, from his experiments on *Dytiscus*, and Ward from those on the crayfish, that the subœsophageal ganglion is

the seat for coördinate movements. Bethe, however, does not regard the subœsophageal ganglion as the centre for coördinate action, since most of the arthropods that he operated on showed few or no disturbances in coördinate movements after its removal. In the grasshopper, as we have seen, the subœsophageal ganglion is not the chief centre for coördinate movements. The destruction of the ganglion is followed by a severe shock effect because it is accompanied by a great loss of blood and necessitates a wound in a sensitive area. The insect can still hop, fly, walk, and right itself, but in an awkward manner, and shortly after the operation it seems to have lost its sense of equilibrium. From the fact, however, that decapitation of the grasshopper does not, as shall shortly be pointed out, destroy coördinate progressive activities, it is evident that the ganglion in the grasshopper does not preside over coördination of these movements, though it may exert some influence over the sense of the position of the body in space.

IV. Decapitation.

The supra and subœsophageal ganglia are removed by cutting off the head. Usually a ligature is tied around the neck before the head is cut off to prevent loss of blood. As was to be expected from the foregoing experiments, the respiration was not materially altered by the operation. It was only decreased in rate. The lack of coordination in the rate of the thoracic and abdominal spiracle movements, however, which may be observed, is not due to any operative disturbance, since, as was said before, this irregularity exists in normal insects.

If a narrow strip of chiten is removed from the side of the abdomen in a decapitated hopper, it is seen that the air-sacs inflate in the inspiratory phase, and that, when the animal struggles, the spiracle movements increase in frequency with the movements of the abdomen and inflation of the air-sacs.

Twenty-four hours after being decapitated, the animal hops and flies four or more feet if it is touched. This depends upon the species; some normally fly further than others.

When it is placed on its back it struggles and turns over, but not so promptly as does the normal one. If, however, it is carefully placed either on its side or back, it will remain so, and, if its feet hold on to a stick, it will not attempt to right itself from any position in which it is placed by changing the

position of the stick. In standing, it may incline more to one side, and often remains in any position in which it has been placed; as, for instance, the thorax touching the table and the abdomen and jumping-legs raised far above it.

It makes purposive reflex movements, though these are not as strong as in the normal hopper, and the power of localization is still left. If any part of the body easily reached by the feet is touched, they attempt to push away the offending object, for instance, if the posterior part of the abdomen is touched with a pencil, first one then the other leg tries to push away the pencil. If the insect is held with the fingers, it struggles to free itself, and, as in the case in the normal hopper, both the abdominal and thoracic spiracles and the abdominal respiratory movements are increased in rate and force. During the first hours it moves, hops and flies spontaneously; that is, without any apparent cause. These movements may be due to operative disturbances. The egg depositors open and close rhythmically and fœces are often excreted, and it often sways from side to side while standing.

The results obtained from this experiment corroborate, in many respects, those already cited. This method of removing the subœsophageal ganglion is very simple and satisfactory, from the fact that all of the ganglion is removed.

V. Removal of Thoracic Ganglia.

The thoracic ganglia are easily exposed on the ventral side. The first is covered by a chitinous plate lying between the first pair of legs. It is successfully destroyed with a hot needle, or can be cut out with a very fine hooked scapel or bent scissors, and the wound covered with shellac. After the shock effect produced by the operation has passed off, the respiratory movements of the abdomen and spiracles continue at about half of the rate observed before the operation. There is, however, complete loss of motion of the first thoracic spiracles, as well as loss of motion and sensation in the first pair of legs. It flies, hops and walks with its second and third pairs of legs, and with the aid of these turns over when placed on its back. Evidently the centre for the turnover reflex is not located in the prothoracic ganglion, as Faivre believed it to be in the water-beetle. When the antennæ are pinched there are no responses in the walking-appendages, and pinching either the second or

third leg produces responses only from these, and fluttering of the wings and wing-covers.

When the second thoracic ganglion is removed, there is a decrease in the rate of respiratory movements, loss of motion in the second thoracic spiracle and of sensation and motion in the second pair of legs, and loss of the power of flight. The animal hops and walks, but does not move the second pair of legs. It tries to turn over if placed on its back, but cannot without its front and jumping-legs. If the antennæ are pinched it uses its front leg to push away the forceps; if the hind legs are pinched it does not push away the forceps, but hops away. Faivre found that the respiratory movements in the water-beetle ceased upon removal of the meso-thoracic ganglion, and only reappeared upon stimulation, and then only when the meta-thoracic ganglion was still intact. My results do not agree with this, since I found that respiratory movements continue without stimulation after extirpation of this ganglion, and the respiratory movements of the abdomen are not greatly changed by the simultaneous removal of this and the meta-thoractic ganglion.

After extirpation of the third thoracic ganglion, only the rate of respiration is affected. Motion and sensation in the third pair of legs are lost, as is also the power of flight. The third thoracic spiracle is inactive. The insect turns over when placed on its back. When the abdomen is pinched the legs remain inactive. It can still make progressive movements with its two pairs of walking-legs.

The air sacs in the thoracic region, even after removal of all the thoracic ganglia, continue to expand and contract with the movements of the abdomen and independently of the thoracic spiracle movements.

VI. Removal of Abdominal Ganglia.

The abdominal ganglia are extirpated from the ventral side of the body by removing a small piece of chitin that lies directly over the ganglia. They were destroyed with a hot needle or extirpated with bent scissors or hooked scalpel. The wound was covered with shellac.

When the first abdominal ganglion is destroyed there is a loss of motion in the first abdominal segment and its spiracles, but all remaining parts of the body continue actively in the

normal manner after about half an hour following the operation, or until all shock effects have worn off. By the removal of the successive abdominal ganglia of the ventral chain like results were obtained, but in addition to these there is a loss of motion in the ovipositor when the last abdominal ganglion was removed.

By severing the longitudinal commissures between different ganglia of the abdominal ventral nerve-cord, or by severing the abdomen from the thorax and cutting it transversely into two or more parts, it is found that the different parts into which the abdomen is divided continue to execute rhythmical respiratory movements, provided the removed piece contains at least three segments. This is in accord with the results obtained by Miss Hyde[8] in *Limulus*.

The respiratory and spiracle movements in the abdomen may stop for a shorter or longer period of time after the abdomen is cut from the thorax, and then spontaneously begin their movements again, or they may continue uninterruptedly but with less frequency and with less force. Moreover, if two drops of a half per cent. curare are injected into the abdomen of a large grasshopper, all voluntary muscles and respiratory movements and spiracles seem paralyzed for from two to six hours. The spiracles are closed, and the abdomen is relaxed in the expiratory phase. This proves that inspiration is due to an active contraction of certain voluntary abdominal muscles.

If a transverse section is made between the third and fourth abdominal segments a small pulsating organ is seen. It is situated close to the ventral side of the body below the alimentary canal and almost directly opposite the heart. I have been unable to determine from literature what it is.

VII. Conclusion.

1. Neither the supraœsophageal ganglia or brain of the grasshopper nor the subœsophageal ganglion, which has been regarded by some authors as analogous to the medulla of vertebrates, is the centre for respiratory movements. Furthermore, the meso-thoracic and meta-thoracic ganglia, which, according to Faivre, presides over the respiration in the water-beetle, *Dytiscus*, do not control the mechanism of the respiratory move-

8. Hyde, I. H., Journal of Morphology, 1897, vol. 9, No. 3, p. 431.

ments in the grasshopper. Each ganglion of the thoracic and abdominal ventral cord is the centre for respiratory movements, and reflex actions of the segment and the appendages to which it belongs. Not only the whole abdomen, but different segments of it will continue their respiratory activity when severed from the body.

2. The posterior part of the brain exerts an inhibitory power over the anterior part of the grasshopper's brain. The anterior part of the brain is the seat for spontaneous progressive locomotion. If the posterior part of the brain is destroyed, leaving the anterior strip of the brain tissue in tact, the animal moves incessantly. If, however, the whole brain is destroyed, the grasshopper stops its progressive movements almost entirely; it takes only a step or two in twenty-four hours.

3. The brain of the grasshopper is the centre for swallowing movements and for inhibiting reflex movements. With the loss of the brain, the animal neither moves its mandibles nor swallows food, and it now responds to subnormal stimuli in an exaggerated way by hopping or flying. Moreover, the palp and preening movements, as well as the rhythmical lifting of the legs are of frequent occurrence, and for no apparent cause.

4. The grasshopper's brain is not the centre for cöordinate movements and direction. Since, when its brain is removed, the insect will respond when stimulated by walking, flying, hopping and righting itself in a normal manner, and will, moreover, move in a direction away from the irritating cause.

5. The brain controls the tonus of the muscles, since after its extirpation, although the grasshopper makes purposive movements to defend itself, it does not do so nearly so powerfully as does the normal animal, and it is very soon fatigued. The position of the head and appendages is altered when the brain is destroyed. The head droops, the flexor muscles of the legs contract, so that the appendages are at first strongly flexed and then extended beyond the normal, due possibly to the contraction of the extensors or inhibition of the flexors. The influence exerted by the brain over the tension of the voluntary muscles is also illustrated by the position of the legs and body, as well as by the direction of progressive movements, when half of the brain is extirpated. During a definite period of time the hopper then inclines more to the side, and moves in a circle toward the un-

injured side, indicating that the flexors of one side and the extensors of the other are affected, and that each half of the brain, though controlling the reflexes of its own side, also exerts to a certain degree a power over the associated muscles of the opposite side.

6. The subœsophageal ganglion is not the center for correlated movements in the grasshopper, as Ward found it to be in the crayfish. Since the turn-over, reflex, walking, hopping, flying and alighting persist not only when it is removed, but when the whole head is cut off. The subœsophageal ganglion exerts, however, to a certain degree, an influence over the sense of equilibrium. The preservation of the segmental arrangement of the nervous system enables the animals to execute the progressive movements.